

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

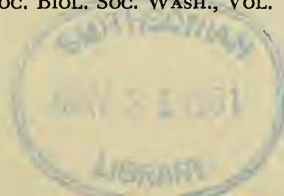
TAXONOMIC NOTES ON THE TUNDRA VOLE
(*MICROTUS OECONOMUS*) IN ALASKA

BY JOHN L. PARADISO AND RICHARD H. MANVILLE

Bureau of Sport Fisheries and Wildlife

This study was undertaken to determine the subspecific status of several hundred Alaskan tundra voles (*Microtus oeconomus*) submitted for identification by the University of Alaska. During the course of the investigation, 1236 specimens were examined, mostly in the collections of the U. S. National Museum. The type specimens of all the named forms have been examined, with the exception of *M. o. punukensis*, for which a good series of topotypes was available. For the loan of specimens in their charge, appreciation is extended to: A. W. F. Banfield, National Museum of Canada (NMC); William H. Burt, Museum of Zoology, University of Michigan (UM); E. Raymond Hall, Museum of Natural History, University of Kansas (KU); Ludwig J. Rowinski, University of Alaska (UA); and Richard G. Van Gelder, American Museum of Natural History (AMNH). This material was deemed sufficient to give a satisfactory picture of the distribution of the Alaskan forms of the species.

Standard cranial measurements were taken with a vernier caliper. The average larger size of males necessitated recording the measurements of the sexes separately, and where two sets of measurements are given, those for the males precede those for females. External measurements were taken in the flesh by the collectors, unless otherwise noted. All measurements are in millimeters unless otherwise stated. Color comparisons were made only on adult specimens in summer pelage. Capitalized color terms are from Ridgway (Color Standards and Color Nomenclature, 1912).



Microtus oeconomus (Pallas, 1776)

Mus oeconomus Pallas, Reise durch Verschiedene Provinzen des Russischen Reichs, III: 693, 1776.

According to Ognev (1944: 165), *Mus oeconomus* of Pallas (1776) is not *Mus oeconomus* of later authors. He suggests that the name was based on a form of *Mus* (*Stenocranius*) *gregalis*, and proposes to use the name *Microtus ratticeps* for the present species. The usage of Ellerman and Morrison-Scott (1951: 705) and other authors such as Vinogradov and Argyropulo (1941: 205), and Kuznetsov (1944: 351) has been followed, however, in retaining the specific name *oeconomus* in this study.

The tundra vole is described by Hall and Cockrum (1953: 423) as varying in total length from about 160 to 225 mm, with a tail length of 36 to 53 mm and a hind foot measurement from 20 to 24 mm. The upper parts vary from dusky gray through rich buff, tawny or cinnamon brown and rusty brown. In all, there is a mixture of black-tipped hairs; sides paler, with the abdomen white, and in some subspecies washed with buff. The tail is bicolored, dusky to black above, whitish to pale buff below. The anterior lower molar (m_1) has only four closed triangles, the fifth triangle being open and confluent with short terminal loop (except in *M. o. sitkensis*, where the fifth triangle is usually closed). The incisive foramina are short and constricted posteriorly.

As pointed out by Zimmermann (1942) and confirmed by Rausch (1950), the species is holarctic in distribution. The differences between specimens from opposite sides of the Bering Sea, in eastern Siberia and western Alaska, are insufficient for specific separation of the two populations. It was found, in fact, that the two populations are so similar that even subspecific separation is questionable.

Geographic variation in the New World forms is slight. Some characters in which significant geographic variation is exhibited are: The size and shape of the auditory bullae; length of upper molar tooththrow; shape of interparietal; slope of occipital plane; coloration; tail length, and over-all size of the animal. In general, it may be said that there is a cline for darker coloration and rounder, more inflated auditory bullae, from west to east. All insular forms examined are larger than mainland forms.

The distribution in Alaska of the ten recognized subspecies is indicated on the accompanying map, p. 83.

Microtus oeconomus operarius (Nelson)

Arvicola operarius Nelson, Proc. Biol. Soc. Wash., 8: 139, 28 December 1893.

Microtus [*oeconomus*] *operarius*, Zimmermann, Arch. f. Naturgesch., 11: 187, 10 September 1942.

Microtus kadiacensis Merriam, Proc. Biol. Soc. Wash., 11: 222, 15 July 1897. (Type from Kodiak Island, Alaska.)

Microtus oeconomus gilmorei Setzer, Proc. Biol. Soc. Wash., 65: 75, 25 April 1952. (Type from Point Lay, 163° 04' W Long. and 69° 46' N Lat., Alaska.)

Type: No. 14379/22225, U. S. National Museum; immature skin and skull, collected at St. Michael, Norton Sound, Alaska, in November 1879, by E. W. Nelson, original number 122.

Distribution: Southern and western mainland Alaska, from Point Lay on the NW coast to Ophir and Takotna on the east, south to the north shore of Prince William Sound, including Kodiak and Afognak Islands.

Coloration: The adult summer pelage of the upperparts is between Snuff Brown and Bister; abdomen pale, grayish white, lightly washed with buff.

Molar tooth pattern: Four closed triangles on m_1 , two inner and two outer, and usually one unclosed inner triangle; m^3 with three triangles, generally closed, with normally three inner and three outer salient angles.

Measurements: The averages and extremes of nine adult males and five adult females from the type locality are as follows: Total length 170 (167–181), 169 (165–176); tail 44 (36–49), 44 (40–48); hind foot 20 (19–22), 20 (19–21); condylobasal length of skull 27.5 (26.8–28.9), 26.3 (25.5–26.9); zygomatic breadth 15.5 (14.8–16.5), 14.8 (14.4–15.0); least interorbital breadth 3.5 (3.2–3.8), 3.4 (3.2–3.5); mastoidal breadth 11.9 (11.6–12.7), 11.3 (11.0–11.7); length of incisive foramina 5.4 (5.0–5.9), 5.1 (4.9–5.2); alveolar length of upper molar toothrow 6.2 (5.9–6.4), 6.0 (5.8–6.4); length of nasals 7.9 (7.5–8.5), 7.3 (6.8–7.7); interparietal breadth 6.7 (5.9–7.8), 7.0 (6.4–7.8); interparietal length 3.5 (3.2–3.9), 3.3 (3.0–3.6).

Measurements of series from Point Lay and from English Bay, Kodiak Island, Alaska, show no significant differences from the topotypes of *M. o. operarius*.

Comparisons: From *M. o. macfarlani*, *M. o. operarius* may be distinguished by its paler coloration, and the following cranial characters: Skull more lightly built; auditory bullae smaller, less inflated, and more elongated antero-posteriorly; mastoidal breadth relatively less; zygomatic arches flaring anteriorly, rather than parallel-sided.

Comparisons of *M. o. operarius* with other Alaskan forms will be found under accounts of those subspecies.

M. o. operarius was compared with specimens of *M. o. tshuktschorum* Miller 1899, from eastern Siberia, to determine the relationships of the two populations of *Microtus oeconomus* from opposite sides of the Bering Sea. The following Siberian material was examined: Cape Shelagskij, 14; East Cape, 4 (NMC); Emma Harbor, 9. The differences between this Siberian material and specimens of *M. o. operarius* from the Seward Peninsula and St. Michael, Alaska, are slight, and the advisability of recognizing them as two distinct subspecies is questionable. If in the future, when more Siberian material is available for a thorough analysis, they prove to be identical, it will be necessary to consider *M. o. tshuktschorum* Miller 1899, as a synonym of *M. o. operarius* (Nelson) 1893. If *M. o. tshuktschorum* Miller, proves to be identical with *M. o. kamtschaticus* Pallas 1778, as Ognev (1944: 168) contends, then *M. o. operarius* (Nelson), would become a synonym of *M. o. kamtschaticus* Pallas.

For the present, however, owing to the geographic separation of the two populations, the lack of Siberian material for a satisfactory analysis, and the disagreement on the names and distribution of the Asiatic forms, it seems advisable to retain the name *M. o. operarius* for the Alaskan population.

Remarks: Setzer (1952) applied the name *Microtus oeconomus gilmorei* to that population of the species which ranges from the "arctic slope of Alaska from Point Lay on the west at least to Umiat on the east, and from the Meade River on the north at least to the crest of the Brooks Range on the south," and designated Point Lay (163° 04' W Long. and 69° 46' N Lat.), Alaska, as the type locality.

Our findings corroborate those of Rausch (1953: 130), who considered *gilmorei* as indistinguishable. The Point Lay material has been examined and found to agree with typical *M. o. operarius* in coloration and in size and shape of the auditory bullae. In fact, the more abundant comparative material of *M. o. macfarlani* and *M. o. operarius* now available shows that many of the diagnostic characters of *M. o. gilmorei* mentioned by Setzer in separating it from *M. o. macfarlani* (longer, narrower auditory bullae; paler, more yellowish coloration; zygomatic arches flaring anteriorly as opposed to nearly parallel-sided) are characters in which *M. o. operarius* differs from *M. o. macfarlani*.

Setzer designated other diagnostic features to distinguish *M. o. gilmorei* from *M. o. macfarlani*, such as: Upper incisors more recurved; maxillary teeth heavier; and skull averaging larger. New comparative material shows that, in these characters, *M. o. gilmorei* falls within the range of individual variation of both *M. o. macfarlani* and *M. o. operarius*.

Bee and Hall (1956: 127) recognize the validity of *M. o. gilmorei*, and give the range as the entire Arctic slope of Alaska. They designate characters to separate it from *M. o. endoecus* (= *macfarlani*) as follows: Smaller size; lambdoidal crest more developed; lachrymal and frontal protuberances sharper; interorbital ridge more pronounced; zygomatic arches thinner; sculpturing of frontal and parietal slightly deeper; and pelage paler.

The paler pelage is a character of *M. o. operarius*, but it is pronounced only in Point Lay specimens. Farther east on the Arctic slope, coloration is as in typical *M. o. macfarlani*. The other characters mentioned either fall within the range of individual variation of both *M. o. macfarlani* and *M. o. operarius*, or are too poorly marked and inconsistent to distinguish *M. o. gilmorei* as a distinct subspecies, and the Point Lay specimens are herein considered to represent *M. o. operarius*.

In southwestern Alaska, the range of *M. o. operarius* includes most of the Alaska Peninsula, and the area as far inland as Ophir and Takotna. Specimens from Kodiak Island and Afognak Island, formerly assigned to *M. o. kadiacensis* Merriam, are indistinguishable from *M. o. operarius* from the type locality.

A specimen from the north shore of Prince William Sound in the collections of the U. S. National Museum, which was the basis for Bailey's

extension of the range of *M. o. yakutatensis* westward to this area (1900: 41) was examined and found to differ in no significant way from *M. o. operarius*. This specimen represents at present the easternmost extension of the range of *M. o. operarius*.

Specimens examined: 441, as follows (all from Alaska, and in the collections of the U. S. National Museum): Afognak Island, Litnik, 7; Becharof Lake, 1; Bethel, 11; Chalitna, 3; Chignik, 6; Chogiung, 12; Cold Bay, 3; English Bay, Kodiak Island, 31; Goodnews Bay, 1; Hooper Creek, 14; Hope, Cook Inlet, 5; Igiak Bay, 10; Iliamna Bay, 3; Iron Creek, 3; Kakhtul River, 4; Kodiak (near), 12; Kokwok River, 45; Kruzgamepa Hot Springs, 2; Lake Aleknegik, 3; Lake Clark, 3; Lake Iliamna (near mouth of Nogheling River), 9; Lake Iliamna (Iliamna Village), 1; Nome, 5; Nome River, 10 miles from coast, 7; Nushagak, 3; Ophir, 1; Point Lay, 27; Point Protection, 5; Prince William Sound (N. shore), 1; St. Michael, 41; Sawtooth Mountains (Kigluaik), 10; Seward, 3; Takotna, 4; Tyoonok, 32; Uyak Bay, 4; Wales Island, 3.

Microtus oeconomus macfarlani Merriam

Microtus macfarlani Merriam, Proc. Wash. Acad. Sci., 2: 24, 14 March 1900.

M[icrotus] oec[onomus] macfarlani, Zimmermann, Arch. f. Naturgesch., 11: 187, 10 September 1942.

Microtus operarius endoecus Osgood, N. Amer. Fauna, 30: 23, 7 October 1909. (Type from mouth of Charlie Creek, Yukon River, about 50 miles above Circle, Alaska.)

Type: No. 9155/37347 U. S. National Museum; adult skin and skull, collected at Fort Anderson, Anderson River, Mackenzie, by R. Macfarlane.

Distribution: Northern and eastern Alaska, Yukon, and Northwest Territories east to Coronation Gulf. In Alaska, the distribution is approximately east of the Utukok River, 200 miles SW of Point Barrow, and the north fork of the Huslia River, south to Mt. McKinley, and Chitina, Alaska, and Kluane in the Yukon.

Coloration: In summer pelage, *M. o. macfarlani* is darker and brighter than *M. o. operarius*. The dorsum is between Mummy Brown and Prout's Brown; pale grayish white, suffused with buff on the abdomen.

Molar tooth pattern: As in *M. o. operarius*.

Measurements: The averages and extremes of 13 males and 19 females from Bettles are as follows: Total length 176 (155-186), 170 (153-188); tail 51 (44-53), 49 (44-54); hind foot 20 (19-21), 20 (19-21); condylobasal length of skull 29.3 (28.0-30.0), 28.5 (27.0-29.5); zygomatic breadth 16.8 (15.6-17.5), 16.2 (15.1-16.9); least interorbital breadth 3.5 (3.2-3.8), 3.5 (3.2-3.9); mastoidal breadth 12.8 (12.4-13.2), 12.5 (12.0-13.1); length of incisive foramina 5.4 (5.0-5.8), 5.3 (4.2-6.0); alveolar length of upper molar toothrow 6.5 (6.0-6.9), 6.6 (6.0-6.9); length of nasals 8.2 (7.9-8.7), 8.1 (7.5-8.7); interparietal breadth 6.9 (5.8-8.9), 6.9 (5.8-7.8); interparietal length 3.4 (3.2-3.8), 3.4 (2.8-4.0).

Eleven males from Tuktoyaktuk, Mackenzie, measure as follows: Condylobasal length of skull 27.9 (26.9–29.9); zygomatic breadth 15.8 (15.1–17.6); least interorbital constriction 3.7 (3.6–3.8); mastoidal breadth 12.5 (12.1–12.9); length of incisive foramina 5.1 (4.7–5.6); alveolar length of upper molar toothrow 6.3 (6.2–6.4); length of nasals 7.6 (6.9–8.4); interparietal breadth 7.1 (6.7–8.0); interparietal length 3.3 (2.9–3.7).

Comparisons: *M. o. macfarlani* differs from *M. o. operarius* in the following characters: Auditory bullae larger, rounder and more inflated; skull heavier, more massive; skull broader in the mastoidal region; zygomata parallel-sided as opposed to flaring anteriorly; teeth larger; and coloration darker and brighter.

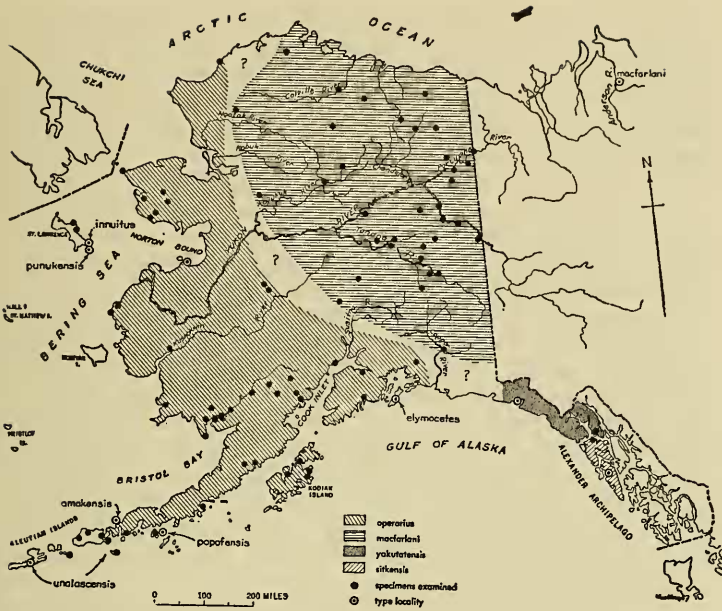
M. o. macfarlani differs from *M. o. yakutatensis* in having a narrower interorbital region; smaller teeth; average smaller and shorter interparietal; less massive skull; and coloration not as dark, and suffused with black.

Remarks: This subspecies is best distinguished near the central portion of its range rather than at the type locality. A large series from Bettles, Alaska, is typical, and is characterized by large, rounded bullae, a broad mastoidal region and dark coloration. Specimens from Circle and Charlie Creek are almost identical. Farther to the east, in the Anderson River region of Mackenzie, which is nearer the type locality of *M. o. macfarlani*, there is a slight but inconsistent tendency toward reduction in the size of the bullae, and skulls average smaller in total length and zygomatic breadth, and are less massive. Nevertheless, the differences are so slight and variable between the Anderson River region specimens and those from Charlie Creek, Alaska (type locality of *M. o. endoeucus* Osgood), that we cannot recognize two subspecies within this range, and *M. o. endoeucus* Osgood is herein considered a synonym of *M. o. macfarlani*.

Specimens assigned by Setzer (1952) to *M. o. gilmorei* from Utukok River (200 miles SW of Point Barrow), mouth of Chandler River, Anaktuvuk Pass, and Umiat and Killik Rivers, were found to agree with *M. o. macfarlani* and are referable to this subspecies. Representative series from the Arctic Slope, designated by Bee and Hall (1956: 135–136) as *M. o. gilmorei*, were examined and are referable to *M. o. macfarlani*, although specimens from the type locality of *M. o. gilmorei* (Pt. Lay, Alaska) are referable to *M. o. operarius*.

Populations of *M. o. macfarlani* that show intergradation with *operarius* in coloration and size and shape of auditory bullae are from the north fork of the Huslia River, Mt. McKinley and Chitina, Alaska.

Specimens examined: 555, as follows: ALASKA: Alatna, 4; Anaktuvuk Pass, 16; Barter Island, 2; Bettles, 42 (part KU); Chandler Lake, 13 (KU); Chandler River (mouth of), 1; Charlie Creek, 14; Chatanika River, 2; Chitina, 2; Black River, 13 (UA); Circle, 19; Driftwood, 12 (KU); Eagle (mountains near), 31; Elliot Highway, mile 13, 4 (UA); Fairbanks, 2; Huslia River (north fork), 13 (UA); Killik River, 3; Lake



Gavia, 20 (KU); Lake Schrader, 3 (KU); Little Moose Creek, 2; McDonald Creek, 1; Meade River, 50.5 mi S and 9 mi W of Point Barrow, 3 (KU); Mt. McKinley, 3; Old John Lake, 32 (UA); Old Rampart, 2 (UA); Paxon Region, Denali Highway, mile 1, 1 (UM); Paxon Region, Richardson Highway, mile 179, 1 (UM); Porcupine Lake, 12 (KU); Porcupine River, 5; Richardson 4; Salcha River (headwaters), 6 (UA); Sheenjek River (near Lobo Lake), 2 (UA); Small Lake, 5 (UA); Tanana Crossing, 24; Tanana River and Clearwater Creek (between), 2 (UA); Umiat (near), 22 (part KU); Utukok River, 200 mi SW Point Barrow, 5.

NORTHWEST TERRITORIES: Aklavik, 3 (NMC); Cape Bathurst, 1 (NMC); Coppermine, 2 (AMNH, NMC); Coronation Gulf, 1 (NMC); Fort Anderson, 5; Horton River, Coal Creek, 2 (AMNH); Langton Bay, 32 (AMNH); mouth of Anderson River, 5 (NMC); Reindeer Station, 1 (NMC); Toker Point, 6 (AMNH); Tuktoyaktuk, 44 (NMC).

YUKON: Burwash Landing, 1 (NMC); Coak Creek (head of), 14; Donjek Bridge, 2 (NMC); Kluane Lake (head of), 2 (NMC); Macmillan Pass, Canol Road, 10 (NMC); Old Crow (near), 20; Rampart House, 25 (NMC); Ross River, Canol Road, 7 (NMC).

Microtus oconomus yakutatensis Merriam

Microtus yakutatensis Merriam, Proc. Wash. Acad. Sci., 2: 22, 14 March 1900.

M[icrotus] oec[onomus] yakutatensis, Zimmermann, Arch. f. Naturgesch., 11: 187, 10 September 1942.

Type: No. 98005, U. S. National Museum (Biological Survey Collection); adult ♂ skin and skull, collected on the north shore of Yakutat Bay, Alaska, on 19 June 1899, by A. K. Fisher, original number 2101.

Distribution: From the north shore of Yakutat Bay, south to Point Gustavus. Also reported at Chitina River Glacier, at about 4500 feet elevation, by Laing, Taverner and Anderson (1929: 102).

Coloration: This is one of the darkest American forms of the species, being nearest to Mummy Brown on the dorsum in summer pelage. The abdomen is heavily washed with ochraceous.

Molar tooth pattern: As in *M. o. operarius*, except that frequently four outer and four inner salient angles are present on m^3 .

Measurements: The averages and extremes of four adult males and nine adult females from the type locality are as follows: Total length 167 (160–172), 160 (152–168); tail 37 (36–38), 37 (35–39); hind foot 21, 20; condylobasal length of skull 29.1 (28.5–39.5), 27.6 (26.7–28.7); zygomatic breadth 16.5 (16.1–16.8), 15.6 (15.0–15.9); least interorbital breadth 3.8 (3.7–3.9), 3.9 (3.9–4.0); mastoidal breadth 13.1 (13.0–13.3), 12.2 (12.0–12.5); length of incisive foramina 5.1 (5.0–5.2), 5.0 (4.8–5.0); alveolar length of upper molar tooththrow 7.0 (6.9–7.1), 6.9 (6.5–7.4); length of nasals 8.0 (7.8–8.2), 7.8 (7.7–8.0); interparietal breadth 7.6 (7.0–7.9), 7.0 (6.8–7.4); interparietal length 4.6 (3.9–5.0), 4.1 (3.9–4.2).

Comparisons: This well-marked subspecies is distinguished from both *M. o. operarius* and *M. o. macfarlani* by its darker coloration and larger molar teeth, as well as its relatively broader mastoidal and interorbital regions.

Remarks: The range of this subspecies has been reported as the "north shore of Prince William Sound" (Bailey, 1900: 40) to Glacier Bay, Point Gustavus. The specimen from the north shore of Prince William Sound was examined and found to be referable to *M. o. operarius*. Specimens from Chitina are referable to *M. o. macfarlani*. Laing, Taverner and Anderson (1929) identified five specimens from Chitina River Glacier, at about 4500 feet elevation, as *M. o. yakutatensis*. These specimens have not been examined, but are presumed to be the ones recorded by Anderson (1947: 200) from near the head of Chitina River, on the west side of Mt. Logan, Alaska. This represents the westernmost, and furthest inland, locality for the subspecies.

Specimens examined: 48, as follows: ALASKA: Glacier Bay, Point Gustavus, 17; Yakutat Bay, 31.

Microtus oeconomus innuitus Merriam

Microtus innuitus Merriam, Proc. Wash. Acad. Sci., 2: 21, 14 March 1900.
M[icrotus] oec[onomus] innuitus, Zimmermann, Arch. f. Naturgesch., 11: 187, 10 September 1942.

Type: No. 99373, U. S. National Museum (Biological Survey Collection); adult ♂, skull only, collected at Northeast Cape, St. Lawrence Island, Bering Sea, Alaska, on 13 July 1899, by C. Hart Merriam.

Distribution: St. Lawrence Island, Alaska.

Coloration: In summer pelage, darker, more reddish brown than *M. o. operarius*; most nearly approaches *M. o. unalascensis*.

Distinctly melanistic individuals have been recorded by Murie (1934) from several localities in the middle portion of St. Lawrence Island. Others have been taken in the hills south of Savoonga, St. Lawrence Island (Murie, 1936: 345).

Molar tooth pattern: As in *M. o. operarius*.

Measurements: Cranial measurements of the type are as follows: Condylbasal length of skull 33.0; zygomatic breadth 19.5; least interorbital breadth 4.2; mastoidal breadth 15.2; length of incisive foramina 6.3; alveolar length of upper molar toothrow 7.4; length of nasals 9.4; interparietal breadth 8.4; interparietal length 3.7.

There are no external measurements for the series in the U. S. National Museum. Hall and Gilmore (1932: 400) give the external measurements of their series as follows: Total length range from 163 to 220; length of tail average 36.1 (extremes 30-48); length of hind foot 22.2 (extremes 21-24).

Comparisons: *M. o. innuitus* differs from *M. o. operarius*, the only mainland form with which it needs comparison, in being darker in coloration and larger in size. The auditory bullae, although similar in shape to those of *M. o. operarius*, are relatively larger. The braincase is more angular and more strongly marked by muscular impressions.

Comparisons with *M. o. punukensis* are included under that subspecies.

Specimens examined: 16 skins and 9 skulls from St. Lawrence Island, Alaska.

Microtus oeconomus punukensis Hall and Gilmore

Microtus innuitus punukensis Hall and Gilmore, Univ. Calif. Publ. Zool., 38: 399, 17 September 1932.

M[icrotus] oec[onomus] punukensis, Zimmermann, Arch. f. Naturgesch., 11: 187, 10 September 1942.

Type: No. 51392, Museum of Vertebrate Zoology; adult ♀, skin and skull, collected on Big Punuk Island, near east end of St. Lawrence Island, Alaska, on 19 August 1931, by Otto Wm. Geist, original No. 2330 R. M. Gilmore.

Distribution: Punuk Islands, Alaska.

Coloration: As in *M. o. innuitus*.

Molar tooth pattern: As in *M. o. operarius*.

Measurements: Cranial measurements of an adult ♀ in the collections of the U. S. National Museum are as follows: Condylbasal length 32.0; zygomatic breadth 17.9; least interorbital breadth 4.1; mastoidal breadth 13.7; length of incisive foramina 5.0; alveolar length of upper molar toothrow 7.4; length of nasals 9.6; interparietal breadth 7.3; interparietal length 3.9.

No external measurements are available for the series in the collections of the U. S. National Museum. Hall and Gilmore (1932) give the ex-

ternal measurements of the type and four female topotypes as follows: Total length 177 (162–196); tail 37.0 (33.0–40.5); hind foot 21.8 (20.0–23.0).

Comparisons: This form is like *M. o. innuitus* in size and coloration, but differs in that the occipital surface of the skull is vertical rather than strongly inclined forward, resembling in this respect *M. o. amakensis* from Amak Island, Alaska. *M. o. punukensis* further differs from *M. o. innuitus* in that, in the former, the interparietal is compressed antero-posteriorly, while in the latter it is large and wedge-shaped.

Specimens examined: 29 from Punuk Island (center island), Alaska.

Microtus oeconomus unalascensis Merriam

Microtus unalascensis Merriam, Proc. Biol. Soc. Wash., 11: 222, 15 July 1897.

M[icrotus] oec[onomus] unalascensis, Zimmermann, Arch. f. Naturgesch., 11: 187, 10 September 1942.

Type: No. 30772/42672, U. S. National Museum (Biological Survey Collection); immature ♀, skin and skull, collected at Unalaska, Alaska, on 13 August 1891, by C. Hart Merriam, original number z.

Distribution: Unimak, Sanak, Tigalda, and Unalaska Islands, Alaska.

Coloration: Summer pelage similar to *M. o. operarius*, but somewhat darker; dorsal portion of tail darker.

Molar tooth pattern: Upper m^3 as in *M. o. operarius*, that is, with three closed triangles, and three inner and three outer salient angles. Lower m_1 with four closed triangles, two outer and two inner. Usually two open triangles are also formed on the inner side of m_1 , but frequently the anterior one is poorly developed, and occasionally it is lacking. The development of the extra unclosed triangle, or loop, on the inner side of m_1 , however, is not confined to this subspecies, but is observed in some specimens throughout the range of the species. It is most frequent, and best developed, however, in the southern part of the range, and especially on Unimak, Sanak and Unalaska Islands.

Measurements: Averages and extremes of seven adult males from Unalaska Island are as follows: Total length (average of three) 170 (162–175); tail (average of three) 39 (35–42); hind foot (average of three) 21 (20–21); condylobasal length of skull 29.6 (27.9–31.0); zygomatic breadth 16.9 (15.5–17.5); least interorbital breadth 3.8 (3.7–4.0); mastoidal breadth 13.1 (12.5–13.9); length of incisive foramina 5.0 (4.7–5.2); alveolar length of upper molar toothrow 7.0 (6.8–7.4); length of nasals 8.0 (7.3–8.4); interparietal breadth 6.8 (6.5–7.5); interparietal length 3.7 (3.2–4.1).

The external measurements of an adult ♀ from Unalaska Island are: Total length 162; tail 46; hind foot 21. Cranial measurements of two adult females are: Condylobasal length of skull 28.6, 28.9; zygomatic breadth 15.2, 16.5; least interorbital breadth 3.8, 3.9; mastoidal breadth 12.5, 12.5; length of incisive foramina 5.2, 5.0; alveolar length of upper

molar toothrow 7.0, 7.1; length of nasals 7.9, 7.8; interparietal breadth 6.1, 7.4; interparietal length 3.6, 4.0.

Comparisons: Externally this form is like *M. o. operarius*, but is darker in comparable pelage, and has a shorter tail, which is more distinctly bicolored. Cranially, *M. o. unalascensis* differs from *M. o. operarius* in that the auditory bullae are larger, more rounded and inflated, resembling the bullae of *M. o. macfarlani*. The teeth are larger than in *M. o. operarius* and approach those of *M. o. yakutatensis* in size.

Remarks: *M. o. unalascensis* was thought to be confined to Unalaska Island, but examination of specimens from Sanak and Unimak Islands shows that they too are referable to this subspecies, although the Unimak specimens exhibit intergradation with *M. o. operarius*. Specimens from King Cove, on the southern tip of the Alaska Peninsula, are intergrades with *M. o. unalascensis* in shape and size of auditory bullae but are referable to *M. o. operarius*.

Specimens examined: 76, from Alaska, as follows: Sanak Island, 5; Tigalda Island, 1; Unalaska Island, 46; Unimak Island: False Pass, 6; Ikatán Peninsula, 4; St. Catherine Cove, 7; Uria Bay, 7.

Microtus oeconomus amakensis O. J. Murie

Microtus amakensis O. J. Murie, Jour. Mamm., 11: 74, 11 February 1930.

Microtus oeconomus amakensis, Hall and Cockrum, Univ. Kansas Publ., Mus. Nat. Hist., 5: 309, 17 November 1952.

Type: No. 246449, U. S. National Museum (Biological Survey Collection); adult ♂, skin and skull, collected on Amak Island, Bering Sea, Alaska, on 8 July 1925, by Donald H. Stevenson, original number 80.

Distribution: Amak Island, Alaska.

Coloration: In summer pelage, almost identical with *M. o. operarius*.

Molar tooth pattern: Like *M. o. operarius* except that frequently four outer and inner salient angles are formed on m^3 .

Measurements: The averages and extremes of three adult males and nine adult females are as follows: Total length 189 (179–198), 181 (168–192); tail 49 (44–53), 48 (38–53); hind foot 22 (21–22), 21 (20–22); condylobasal length of skull 29.8 (29.3–30.6), 28.7 (27.9–29.9); zygomatic breadth 17.3 (17.0–17.7), 16.2 (15.8–17.0); least interorbital breadth 4.0 (3.8–4.2), 3.9 (3.8–4.1); mastoidal breadth 13.2 (12.7–13.8), 12.7 (12.2–13.0); length of incisive foramina 4.6, 4.3 (4.0–4.8); alveolar length of upper molar toothrow 6.8 (6.7–6.9), 6.8 (6.5–7.2); length of nasals 8.4 (8.3–8.5), 8.1 (7.8–8.4); interparietal breadth 6.9 (6.7–7.2); 7.0 (6.4–7.5); interparietal length 4.1 (3.8–4.5), 3.9 (3.4–4.4).

Comparisons: Externally this form is like *M. o. operarius*, but differs in that the upper part of the tail and hind feet are paler. Cranially, *M. o. amakensis* averages larger, and has a flattened, vertical occipital surface. The incisive foramina are shorter and more opened than in *M. o. operarius*.

Specimens examined: 33 from the type locality.

Microtus oeconomus popofensis Merriam

Microtus unalascensis popofensis Merriam, Proc. Wash. Acad. Sci., 2: 22, 14 March 1900.

M[icrotus] oec[onomus] popofensis, Zimmermann, Arch. f. Naturgesch., 11: 187, 10 September 1942.

Type: No. 97956, U. S. National Museum (Biological Survey Collection); adult ♂, skin and skull, collected on Popof Island, Shumagin Islands, Alaska, on 16 July 1899, by W. E. Ritter, original number 2200.

Distribution: Known from Popof and Unga Islands, Alaska.

Coloration: As in *M. o. operarius*.

Molar tooth pattern: Similar to *M. o. unalascensis* in that usually two open triangles are formed on the inner side of m_1 ; frequently, however, the anterior one is poorly developed or is lacking. Upper m^3 is as in *M. o. operarius*.

Measurements: Cranial measurements of the type are as follows: Condylbasal length of skull 31.0; zygomatic breadth 17.6; least interorbital breadth 3.9; mastoidal breadth 13.4; length of incisive foramina 5.9; alveolar length of upper molar tooththrow 7.2; length of nasals 9.0; interparietal breadth 7.0; interparietal length 4.4.

A female from the type locality measures as follows: Total length 189; tail 42; hind foot 23; condylbasal length of skull 32.4; zygomatic breadth 18.6; least interorbital breadth 3.8; mastoidal breadth 14.0; length of incisive foramina 7.0; alveolar length of upper molar tooththrow 7.4; length of nasals 9.2; interparietal breadth 7.3; interparietal length 4.6.

A male from Unga Island has the following cranial measurements: Condylbasal length of skull 32.3; zygomatic breadth 18.7; least interorbital breadth 3.5; mastoidal breadth 14.3; length of incisive foramina 6.1; alveolar length of upper molar tooththrow 7.4; length of nasals 8.8; interparietal breadth 7.8; interparietal length 3.8.

Comparisons: *M. o. popofensis* differs from *M. o. operarius* in larger size, and in having blunter, more rounded and inflated auditory bullae.

It differs from *M. o. unalascensis* as follows: Paler coloration; larger size; auditory bullae smaller and less inflated; incisive foramina more open anteriorly.

Specimens examined: 23, from Alaska, as follows: Popof Island, 11; Unga Island, 12.

Microtus oeconomus elymocetes Osgood

Microtus elymocetes Osgood, Proc. Biol. Soc. Wash., 19: 71, 1 May 1906.

M[icrotus] oec[onomus] elymocetes, Zimmermann, Arch. f. Naturgesch., 11: 188, 10 September 1942.

Type: No. 137323, U. S. National Museum (Biological Survey Collection); adult ♂, skin and skull, collected on the east side of Montague Island, Prince William Sound, Alaska, on 12 May 1905, by C. Sheldon, original number 8(5448-X).

Distribution: Montague Island, Alaska.

Coloration: Most nearly approaches *M. o. yakutatensis* in summer pelage. The underparts are considerably suffused with buff, and are darker than in *M. o. operarius*.

Molar tooth pattern: Lower m_1 as in *M. o. operarius*, with four enclosed loops or triangles on m^3 , five of the specimens examined having three inner and four outer salient angles, and two specimens having four inner and four outer salient angles.

Measurements: The type specimen and three adult males measure as follows: Condylbasal length of skull 31.7 (31.2–32.7); zygomatic breadth 17.9 (17.2–18.6); least interorbital breadth 3.8 (3.6–4.0); mastoid breadth 13.4 (13.0–13.7); length of incisive foramina 5.7 (5.4–5.8); alveolar length of upper molar toothrow 7.2 (7.1–7.3); length of nasals 8.5 (8.1–9.2); interparietal breadth 6.9 (6.3–7.4); interparietal length 3.8 (3.2–4.4).

The external measurements for the series in the collections of the U. S. National Museum could not be located. Osgood (1906), however, gives external measurements for the type and two topotypes as follows: Total length 201, 191, 180; tail 40, 40, 35; hind foot (dry) 23.5, 23, 22.

Comparisons: From *M. o. operarius*, *M. o. elymocetes* differs in being larger and darker.

It is similar to *M. o. yakutatensis*, from which it may be distinguished by its larger size.

Remarks: Heller (1910: 342–343) found this vole abundant on Montague Island. He estimated that there was perhaps not a square rod of ground on the island without its runways. The largest specimen he collected exceeds considerably in size any of Osgood's material. His largest specimen, an adult female, measures: Total length 255; tail 49, hind foot 24.

Heller says that this island form is easily distinguished from any other form inhabiting the region by its larger size and darker coloration, the buffy wash on the underparts being heavier than in allied forms.

Specimens examined: 7, from the type locality.

Microtus oeconomus sitkensis Merriam

Microtus sitkensis Merriam, Proc. Biol. Soc. Wash., 11: 221, 15 July 1897. *M[icrotus] oec[onomus] sitkensis*, Zimmermann, Arch. f. Naturgesch., 11: 187, 10 September 1942.

Type: No. 73839, U. S. National Museum (Biological Survey Collection); immature ♂, skin and skull, collected at Sitka, Alaska, on 3 August 1895, by C. P. Streater, original number 4745.

Distribution: Baranof and Chichagof Islands.

Coloration: Similar in summer pelage to *M. o. yakutatensis*.

Molar tooth pattern: Usually five closed triangles on m_1 instead of four; m^3 has three closed triangles and generally four inner and four outer salient angles.

Measurements: An adult female from Sitka measures as follows: Total length 190; tail 45; hind foot 22; condylbasal length of skull 29.2; zygomatic

matic breadth 16.0; least interorbital breadth 3.9; mastoidal breadth 12.4; length of incisive foramina 5.4; alveolar length of upper molar toothrow 7.2; length of nasals 7.7; interparietal breadth 7.2; interparietal length 3.7.

An adult male from Mud Bay, Chichagof Island, measures as follows: Total length 190; tail 43; hind foot 21; condylobasal length of skull 31.7; zygomatic breadth 18.2; least interorbital breadth 4.3; mastoidal breadth 13.7; length of incisive foramina 6.2; alveolar length of upper molar toothrow 7.2; length of nasals 8.7; interparietal breadth 6.9; interparietal length 4.0.

Comparisons: This subspecies closely resembles *M. o. yakutatensis*, both cranially and in coloration. It is larger, however, and has longer, narrower incisive foramina, and usually an extra closed triangle on m_1 .

It differs from *M. o. operarius* and *M. o. macfarlani* in being larger in size and darker in coloration, as well as in having the extra closed triangle on m_1 .

Specimens examined: 3, from Alaska, as follows: Mud Bay, Chichagof Island, 1; Sitka, 2.

LITERATURE CITED

- Anderson, Rudolph Martin. 1947. Catalogue of Canadian Recent mammals. Bull. Nat. Mus. Canada, 102: 200.
- Bailey, Vernon. 1900. Revision of American voles of the genus *Microtus*. N. Amer. Fauna, 17: 1-88.
- Bee, James W. and E. Raymond Hall. 1956. Mammals of northern Alaska on the Arctic slope. Univ. Kansas Mus. Nat. Hist., Misc. Publ., 8: 1-309.
- Ellerman, J. R. and T. C. S. Morrison-Scott. 1951. Checklist of Palaearctic and Indian mammals, 1758-1946. Brit. Mus. (Nat. Hist.): 1-810.
- Hall, E. Raymond and E. Lendell Cockrum. 1953. A synopsis of the North American microtine rodents. Univ. Kansas Publ., Mus. Nat. Hist., 5(27): 373-498.
- and Raymond M. Gilmore. 1932. New mammals from St. Lawrence Island, Bering Sea, Alaska. Univ. Calif. Publ. Zool., 38: 391-404.
- Heller, E. 1910. Mammals of the 1908 Alexander Alaska Expedition and descriptions of the localities visited and notes on the flora of the Prince William Sound region. Univ. Calif. Publ. Zool., 5: 321-360.
- Kuznetsov, B. A. 1944. Ordo Rodentia. Pp. 262-368 in Bobrinskii, N. A., B. A. Kuznetsov and A. P. Kuzyakin: Mammals of USSR. Moscow. 1-440.
- Laing, H. M., P. A. Taverner and R. M. Anderson. 1929. Birds and mammals of the Mount Logan Expedition, 1925. Bull. Nat. Mus. Canada, 56: 69-107.
- Miller, Gerrit S., Jr. 1899. Description of a new vole from eastern Siberia. Proc. Biol. Soc. Wash., 13: 11-12.

- Murie, Olaus J. 1934. Melanism in an Alaskan vole. *Jour. Mamm.*, 15: 323.
- . 1936. Notes on the mammals of St. Lawrence Island, Alaska. Appendix III, pp. 337-346 in Geist, O. W. and F. G. Rainey: Archaeological excavations at Kukulik. Misc. Publ. Univ. Alaska, 2: xviii + 391.
- Ognev, S. I. 1944. Contributions to the taxonomy of *Microtus ratticeps* Keyserl. et Blas. *Comp. Rend. (Doklady) de l'Acad. Sci. de l'URSS*, 44(4): 165-168.
- Osgood, Wilfred H. 1906. A new vole from Montague Island, Alaska. *Proc. Biol. Soc. Wash.*, 19: 71-72.
- Pallas, P. S. 1778. *Novae species quadrupedum e glirium ordine*. Erlangen. Pp. 1-388.
- Rausch, Robert. 1950. Notes on microtine rodents from the Brooks Range, arctic Alaska. *Jour. Wash. Acad. Sci.*, 40(4): 133-136.
- . 1953. On the status of some Arctic mammals. *Arctic*, 6: 91-148.
- Setzer, Henry W. 1952. A new subspecies of *Microtus oeconomus* from Alaska. *Proc. Biol. Soc. Wash.*, 65: 75-76.
- Vinogradov, B. S. and A. I. Argyropulo. 1941. *Tableaux analytiques de rongeurs*. Faune de l'URSS, new series, No. 29: 1-241. Moscow.
- Zimmermann, Klaus. 1942. Zur kenntnis von *Microtus oeconomus* (Pallas). *Archiv f. Naturgesch.*, Leipzig, n. f., 11(2): 174-197.